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An Area-Per-Individual (API) Model For Estimating Critical Habitat Requirements In Aquatic Species-At-Risk.

Modèle de la superficie par individu pour évaluer les besoins en habitat critique chez les espèces aquatiques en péril.

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ABSTRACT

Identifying and mapping critical habitats will be a primary element in efforts to protect and restore of Canada's aquatic species at risk once minimum safe population sizes are established. A simple multi-stage population model for freshwater fishes is presented as a basis for estimating how much habitat will be needed. Spawning, yoy, and one+ life stages are considered. Links between area-per-individual (API) of available suitable habitat and life stage processes provide a means for estimating habitat requirements and identifying potential productivity bottlenecks. Life history strategy affects the dynamics of populations and the patterns of life-stage habitat requirements. How habitat quality can affect population success is examined. Results are presented for representative freshwater fish species (lake charr which is well known and deepwater sculpin which is a poorly known species-at-risk). Approaches to the estimation of API are explored. The model may be extended to more complex life histories and should be broadly applicable to other aquatic species-at-risk.

RÉSUMÉ

L'identification et la cartographie des habitats critiques seront des éléments importants des efforts visant à protéger et à rétablir les espèces aquatiques en péril du Canada lorsque l'effectif minimal raisonnable de la population a été atteint. Un modèle démographique simple à plusieurs stades de développement pour les poissons dulcicoles est présenté comme base pour évaluer la quantité d'habitat requise. Les stades pris en compte sont les reproducteurs, les jeunes de l'année et les poissons d'âge 1+. Les liens entre la superficie par individu d'habitat convenable disponible et les processus du cycle biologique permettent d'évaluer les besoins en habitat et de déterminer les obstacles potentiels à la productivité. La stratégie du cycle biologique modifie la dynamique des populations et les tendances des besoins en habitat selon le stade du cycle biologique. On examine de quelle façon la qualité de l'habitat peut influer sur le succès de la population. Les résultats sont présentés pour des espèces de poissons dulcicoles représentatives (le touladi, espèce bien connue, et le chabot de profondeur, qui est une espèce en péril mal connue). On étudie les méthodes d'évaluation de la superficie par individu. Le modèle peut être élargi à des cycles biologiques plus complexes et devrait être applicable en général à d'autres espèces aquatiques en péril.

Introduction

Successful implementation of Canada's Species-At-Risk Act (SARA) will hinge on the identification and protection of habitats critical to all life stages of each listed species. The population required to conserve and potentially delist a SARA species will depend on life history characteristics, and likely the metapopulation structure of the species stock. Once the target population numbers have been estimated, the amounts and locations of essential habitats will have to be estimated. Essential habitats maybe legally deemed "critical habitats" as defined in SARA once precise rules and methodologies have been agreed. The purpose of this paper is to present a prototype model that may provide a means for estimating the amount of essential habitat needed given population targets.

Fahrig (2001) has stated the basic question addressed here, "how much habitat is enough", in considering how life history characteristics affect the answers obtained. All populations are ultimately constrained, directly or indirectly, by the supply of their suitable habitat. The supply may directly affect key life history process rates, fecundity, survival, and growth, and thereby determine the size and structure of a population. Supply may indirectly affect a population by providing a template for biotic interactions such as predation and parasitism.

In population ecology, there is well-established allometric relationship between population density and body mass (cf Blackburn et al. 1990). As the slope of the log-log relationship typically is close to –0.75, the phenomenon is widely interpreted as reflecting underlying energy metabolic rates of individuals, resulting in the energetic equivalence rule whereby populations within a community, regardless of body mass, use equal amounts of energy (Griffiths 1992). These relationships have been demonstrated in aquatic communities (Cyr et al. 1997) and in fish populations (Boudreau and Dickie 1989; Randall et al. 1995). A similar allometric relationship has been shown in fish for home range versus body mass (Minns 1995). Minns et al. (1996) used the allometric relationships in a population model of northern pike, *Esox lucius*, a model where growth and survival rates were linked by life stage to measures of habitat supply. The inverse of the population size- body mass relationship provides an estimate of the area-per-individual (API) required by the members of a population. Since population density estimates are generally made in healthy populations occupying preferred habitat, the API values should provide a reasonable estimate of the area required to attain expected growth and survival rates. The API relationship should be applicable in modelling population process rates in larval, juvenile, and adult fish.

Spawning-egg incubation is another life stage when habitat space may become limiting. Fishes often have specialized spawning habitat requirements and often aggregate in high densities to spawn. Nesting species typically prepare a nest area and there will be an upper limit to nest packing in preferred spawning habitats. Where spawners merely aggregate, there is evidence of negative interactions if fish become too closely packed. Hence, it is reasonable to assume that there is a preferred area-per-spawning female in preferred habitat necessary to maximize the likelihood of success for eggs laid there. Eggs per se, given their small size require very little area-per-individual. When excess eggs are laid in preferred habitats or if eggs are laid in non-preferred habitats, hatching success often declines significantly.

These area-per-individual (API) phenomena provide the basis for population models for use to estimate habitat requirements of all fish populations and especially of species-at-risk.

API model

The population model presented here is a simplified version of a northern pike, *Esox lucius*, population model developed by Minns et al (1996). The model consists of three life stages: spawning to egg hatch, hatched eggs to age 1 (yoy), and all ages aged 1 and older at the start of the spawning season (one+). The model also has much in common with Moussali and Hilborn's (1986) model based on productivity and carrying capacity in salmonid stocks. At each life stage, there is a maximum potential survival rate that is achievable when the habitat area per individual (API) is equal to or exceeds the minimum specified (Figure 1). The habitat supply for each life stage is estimated using a weighted suitable area (WSA) approach which is conceptually based the habitat suitability index (HSI) model used in the United States Fish and Wildlife Service's Habitat Evaluation Procedures (HEP) (Terrell et al 1982). The HSI approach provides the conceptual basis for much of Fisheries and Oceans Canada's Fish Habitat Management decision-making in Canada. Thus, the model presented here has two components: one that describes the supply of suitable habitat (area•suitability), and one that describes the population dynamics of a species in a finite space with habitat supply potentially influencing population size and persistence.

For each life stage (i), I assume that the ecosystem area is divided into three types of habitat: a proportion (p_{hi}) that is highly suitable (h_{hi} = 1.0), a proportion (p_{si}) that is somewhat suitable (0.0 > h_{si} > 1.0), and a proportion (p_{ui}) that is unsuitable (h_{ui} = 0.0) (Table 1). The proportions of area sum to 1.0. In the first instance, I assume that a larger area of somewhat suitable habitat can be equivalent to a smaller area of highly suitable habitat in determining the potential habitat supply for successful survival through each life stage. The weighted suitable area (WSA), equivalent to an area of highly suitable habitat, equals $W_i = A_T \cdot (p_{hi} \cdot h_{hi} + p_{si} \cdot h_{si})$.

In the population model, I begin with the spawning season. The female spawning population size consists of r percent of all mature animals aged m or older, N_m, where r is the percentage of females in the mature population and m is the age at maturity (Table 2):

$N_m = r \cdot \sum N_i$, $i = m$ to maximum age.

Size at age is not represented explicitly in this prototype model. The potential number eggs per female spawner, F, is estimated using available data and represented as an average per individual expected from a stable post maturation age structure.

I assume that each female spawner requires a minimum area of suitable habitat (a_s) to achieve the maximum potential hatching success of eggs laid. In the total ecosystem with area A_T, The available area per spawner, As, is then computed as $W_s/(r \cdot N_m)$. If A_s is >= a_s then the survival from egg deposition to hatch is the maximum, s_s. If A_s is < a_s then the survival is decreased in proportion to the ratio of A_s/a_s. The basic equations are as follows:

$N_e = f \cdot r \cdot N_m$

$N_h = s_s \cdot N_e$ if $A_s >= a_s$ <u>or</u> $s_s \cdot N_e \cdot A_s/a_s$

A similar approach is taken for survival of young-of-the-year from hatch to age with area per hatched egg, A_y, estimated from W_y/N_h :

$N_y = s_y \cdot N_h$ if $A_y >= a_y$ or $s_y \cdot N_h \cdot A_y/a_y$

Finally the same approach is followed for the one+ population, N_o, with the addition of N_y as recruits at age one with area per one+, A_o, estimated from W_o/N_o:

$N_o(t+1) = N_y(t) + (s_o \cdot N_o(t)$ if $A_o >= a_o$ or $s_o \cdot N_o(t) \cdot A_o/a_o)$

In practice, each age class from age 1 to the maximum age is tracked. Each year, the survivors from age i pass to age i+1 except for the maximum age class, which gets survivors from ages maximum and maximum-1. Given the age of maturation (m), the numbers of mature animals can be computed.

Given freshwater fish as a reference context, there are a number of *a priori* truisms and expectations that can influence model predictions:

- Population numbers:
  - Numbers will generally decrease through life stages, $N_e > N_h > (N_y$ and $N_o)$. In long-lived species, N_o may exceed N_y, annual recruitment.
  - Numbers of one+ will always exceed mature numbers, $N_o > N_m$, assuming no immigration.
- Survival rates"
  - Survival from hatch to age 1 will be much lower that egg hatching success and one+ annual survival, (s_e and s_o) >> s_y, as is generally observed in fishes.
  - Maximum egg hatching success will often exceed one+ annual survival, $s_e > s_o$
- Area per individual (API):
  - API will increase through the life stages and the areas required per spawner and egg will be must less than those for yoy and one+, (a_o and a_y) >> a_s >> a_e. This is consistent with the well-known self-thinning hypothesis for stream salmonids.
  - API for one+ will be larger than for yoy, $a_o > a_y$
- Suitable habitat supply:
  - Within species life stages often have little overlap spatially or temporally, W_s, W_y and W_o are approximately additive. This represents ontogenetic habitat shifts though the generality of these shifts has not been fully documented.
  - The total ecosystem is unlikely to be suitable for any or all life stages, ($W_s + W_y + W_o$) < A_T

These expectations are examined in the case studies presented below but will require much further evaluation.

Implementation and testing

The implementation of an API model for any species requires that estimates be obtained for all the key parameters. The life history parameters are the grist of many fish population and ecology studies and hence should be obtainable from literature in the first instance. The area per individual requirements may present more difficulty.

Life history and API parameter estimation

The area-per-individual estimates for the life stages hatch to age 1 and one+ were estimated using the population density- body size relationship derived for lake fish by Randall et al. (1995) and used previously in the pike model of Minns et al. (1996). The equation is:

(1) API (m^2) = $e^{-10.37} \cdot L^{2.58}$ (length in mm)

For one+, the area per animal was estimate for two body sizes, at maturity and at maximum, numbers that are widely available for freshwater fish (Randall and Minns 2000; Coker et al. 2001). As fish numbers typically decline geometrically through age classes, the geometric mean of the API at maturity and maximum size was used for all one+ fish. Similarly for hatch to age 1, API was estimated from the same allometric relationship for two size, fry at

emergence and juveniles at age 1, and a geometric mean computed. This approach was used in both case studies here.

Estimates of area per spawning female were obtained from literature reviews where possible. Otherwise, simple assumptions based on a radius proportional to body length were used to estimate an area as was done by Minns et al. (1996) in the pike model.

Estimates of egg hatching success under ideal conditions are often available from experimental studies and provide the estimates of s_e. Mean fecundity per mature female can be estimated from an allometric fecundity-body size relationship by taking the geometric mean of estimates for mature and maximum body sizes.

Fisheries investigations typically generate estimates of mean annual survival for one+ or older fish where recruitment to sampling gear or fisheries occurs at a later age. A recent compilation by Lorenzen (1996) provides an example of how an estimate of annual survival might be obtained. Earlier, Pauly (1980) provided an approach based on growth parameters and in situ temperatures.

Estimates of survival from hatch to age 1 are often the most difficult to obtain though there are instances in the literature. If no direct estimate is available, a preliminary estimate can be obtained by simulating a stable one+ population with constant annual survival. Size at age is estimated from empirical observations or a Bertalanffy growth equation. Fecundity per age class is estimated from a combination of eggs-body size function, percent mature, percent female, and age class number. Summed across all age classes the annual potential egg output can be estimated. After applying a survival rate to hatch, the ratio of numbers at age 1 to egg hatched gives a first order estimate of survival. This survival can be used as a starting point for population modelling.

Population modelling

In each case study, a population model was set up using Microsoft Excel spreadsheets. Nominal populations were established in year 0 and the models run with fixed parameter values for 100 cycles and the population values in year 100 were taken as the reference output values. Graphs of population size versus time were examined to ensure that the population had reached a steady state. Four population size indicators were computed: number of eggs hatched (N_h), number of yoys reaching age 1 (N_y), number of one+ individuals (N_o), and number of mature individuals (N_m).

Suitable habitat supply

To assess the API models, I used two approaches. First, I ran the models assuming that the total area of the ecosystem was suitable for all life stages ($p_{hi} = 1.0$). Second, I used observations of habitat use to make first order estimates of the proportion of the ecosystem suitable for each life stage and ran the model with those estimates.

Parameter sensitivity analysis

Since the API component of the population model is the novel feature, I focused the sensitivity analysis on uncertainty in life stage API values. The baseline estimates of a_i values with the two habitat supply profiles were used to establish reference population metric values. Then I performed runs where each a_i in turn was reduced by 50% or increased by 100%.

Life stage sensitivity to reduced habitat supply

Having established two population predictions using the total and best estimate habitat supplies, I examined how reductions in habitat supply by life stage affects the predicted population size. I chose to assess how much habitat supply would have to be reduced to reduce the population size to 95% of the reference value. As interactions among life stage habitat supplies may affect population outcome, I examined the 95% target for each of the four population indicators.

Case studies

I selected two species as subjects for prototype applications of this API model: lake charr, *Salvelinus namaycush,* whose life history is known very well, and deepwater sculpin, *Myoxocephalus thompsoni,* which is a species-at-risk (SAR) and less well-known. It is easier to obtain estimates of key parameter values for more studied species as population studies have often been undertaken. Non-SAR species with similar life history characteristics should be able provide the initial basis for estimating habitat requirements when SARs are poorly known.

Results

Lake charr (*Salvelinus namaycush*)

Lake charr is a long-lived species with late maturation that has relatively low fecundity. These life history traits are similar to those seen in some SAR. It occurs in deep oligo- to meso-trophic lakes across Canada particularly along the southern portion of the boreal region. The species exhibits considerable variation in its life history across its distribution (Shuter et al 1998). A recent paper by Mills et al (2002) provides detailed population information for several small lake charr populations in lakes at the Experimental Lakes Area (ELA) in northwestern Ontario and provides a suitable focus for a case study analysis.

Shuter et al. (1998) provide estimates of all the key life history rates with equations indicating how lake properties affect values (Table 3). Estimates of mean annual one+ survival in unexploited populations at ELA came from Mills et al. (2002). I used typical ELA lake properties to define various parameters. John D. Fitzsimons (personal communication) provided information on fry size at emergence, egg hatching success and spawning areas from field and laboratory results and experience. Weights at maturity and maximum were estimated and the geometric mean used as an indicator of one+ mean weight. The fecundity rate was adjusted to that for the mean one+ weight. The upper bound of the survival to age 1 was used as the estimate in the population model. The API values were estimated from Randall et al. (1995) for emergent fry and age 1 and the geometric mean taken as the model value for survival from hatch to age 1. API values at maturity and maximum sizes were estimates and the geometric mean taken as the value for one+ animals. Age at maturity was set at 6 years in the model and the maximum age set to 20.

For modelling purposes I assumed a lake of 25 ha with mean and maximum depths of 10 and 20 metres, typical of values at ELA (Brunskill and Schindler 1971) (Table 4). Using the hypsometric equation of Minns et al. (1996) areas between any two depth contours can be estimated with the mean:maximum depth ratio defining a shape constant for the lake. From Fitzsimons (1994) analysis, spawning would be expected to occur between 0.5 and 1.5 metres. This area was taken as the estimate of spawning habitat. The main growing habitat for one+ lake trout is in the hypolimnion during the summer. Since thermocline depths are typically around 5 metres in ELA lakes, I took the area between 5 and 20 metres as the estimate of one+ habitat. Fry gradually move off the spawning shoals in the spring and gradually move deeper as they grow. Since adult lake trout are cannibalistic and yoy should try to avoid predation,

I assumed that the yoy habitat lay between 1.5 and 5 metres. These habitat areas were used as the best baseline values for the model simulations.

Using the total and best habitat supply inputs, populations were simulated and four population metrics determined in each scenario, number of eggs hatched (N_h), number of age 1 recruits (N_y), number of one+ individuals (N_o), number of mature individuals (N_m) (Table 2). The percentage of the ecosystem area (A_T) available as high suitability habitat is shown in each case for spawning (p_{hs}), young-of-the-year,yoy, (p_{hy}), and one+ individuals (p_{ho}) (Table 1). Interestingly, the best estimate habitat supply produces larger number of eggs hatched and mature individuals but smaller numbers of yoy and one+ compared to the total supply inputs (Table 5). The numbers generated for a 25 ha lakes are not too dissimilar to values reported by Mills et al. (2002) for ELA lakes. As expected the simulated populations are very sensitive to estimates of API especially for one+ and yoy stages (Table 5). In the total baseline scenario, population numbers are most sensitive to changes in one+ API and only slightly affected by changes in yoy API. In the best estimate baseline scenario both one+ and yoy APIs have an impact. The difference between the two baseline values are due to the relative supplies of yoy and one+ habitats. Changes in the spawning API had no effect in either scenario.

The changes in habitat supply needed to reduce population indicators to 95% of their baseline value varied considerably and showed the role of shifting life stage bottlenecks (Table 6). In the total baseline scenarios, the spawning habitat supply has to be reduced to 0.019% or less to effect the 5% reduction in population indicators (Table 6). The yoy habitat has to be reduced to about 7% (N_h and N_m) or 45-51% (N_y and N_o) of total depending on the population indicator chosen. Changing yoy habitat supply can affect whether yoy or one+ habitat is controlling population size. The one+ supply change has a linear effect on population outcomes. These results indicate that one+ habitat is the dominant supply variable. In the best estimate baseline, dominance shifts to yoy habitat supply as changes in relative availability are factored into the prediction of population size. Spawning habitat has to be reduced to 0.3 to 2.2% of the best estimate to reduce population size by 5%. The yoy habitat supply response is linear here, given yoy habitat is in relatively short supply to begin with. The one+ response is stronger with 30 to 82% of supply giving the 5 percent reduction. Yoy habitat supply is most limiting in the best baseline scenario but one+ supply still has a major effect. In neither baseline does spawning habitat supply have a major effect.

These results also indicate the complexity of choosing a population indicator as a benchmark for tracking success. Changes in relative habitat supply by life stage can affect the population outcome by shifting bottleneck control between life stages, making choosing a single population indicator risky. While spawning habitat appears least likely to be limiting this does not mean it can be ignored since if spawning site selection has a genetic component loss of a small but essential piece of habitat might be terminal for a population. As a final test, the life stage habitat supply thresholds were all set to their 95% values simultaneously in both the total and best scenarios. and the outcomes expressed as a percentage of the baseline values (Table 7). In the unrealistic total habitat supply scenario the recruitment at age 1 and the total one+ population size is reduced by large amounts while eggs hatched and the mature population size are relatively unchanged. In the best scenario, hatched eggs are the most affected. Neither of these outcomes is likely to be acceptable as risks in defining essential habitat supply.

Deepwater sculpin (*Myoxocephalus thompsoni*)

Deepwater sculpin is a COSEWIC-listed species in Canada about which comparatively little is known (Parker 1988). The four-horned sculpin, *Myoxocephalus quadricornis*, is a closely related species occurring in marine, estuarine and some glacial relict lake environments and some of its life history information has been used to fill gaps in the deepwater sculpin profile.

Selgeby (1988) provided a life history overview of three sculpin species in Lake Superior. From this report I obtained a length-weight relationship, estimates of maximum size, size at maturity, size at age 1 and size of emerging larvae, and age at maturity (Table 8). Parker (1988) reports information on the sex ratio and fecundity. Lacking any data on egg hatching success, I assumed it was 90% as with lake trout. Selgeby (1988) reported a total mortality rate for older sculpins from which I estimated annual survival.

For survival from egg hatch to age one, I used a steady state calculation to obtain an initial estimate. Dryer (1966) reported average catches of 35 per tow of one+ deepwater sculpin with a 31 foot headrope trawl towed for 15 minutes at 3 miles per hour in depths > 50 m. If this catch is multiplied out for the 50-100 m in a 1000 ha lake, the population size is 20060. I assumed this population was age 2+ and applied Selgeby's survival rate to assign numbers to age classes. I hindcast numbers of individuals at age 1. Assuming the fecundity from Parker applied to age 3+ animals, I estimated egg production and applied a 90% survival rate. Then I calculated the nominal survival rate from hatched egg to age 1 as 0.03 from the ratio of hatched eggs to number at age 1 (42092). Mansfield et al. (1983) reported deepwater sculpin larval densities of 5-78 per 1000 m3 in inshore waters in the 8 to 18 metre contours of Lake Michigan. Taking the geometric mean density and volume inshore between 8-18 m in the case study lake of 1000 ha, gives a larval population of 46080.

The Randall et al. (1995) equation for density versus size underestimates the area per individual needed for young-of-the-year and one+ animals in deepwater sculpin since they are generally found in larger, deeper, and much less productive lakes. Sculpins are benthivorous and live at great depths. Macrobenthic biomass typically decreases exponentially with depth in lakes (Brinkhurst 1974). Rasmussen and Kalff (1987) developed empirical models for zoobenthos in lakes. Those models showed that benthos in three bathymetric zones were correlated positively with chlorophyll and total phosphorus concentrations and negatively with Secchi depth. In addition, mean lake depth and sample depth within lakes were negatively correlated with benthic biomass. As environmental temperatures are lower at greater depths in lakes, P:B ratios are lower thereby leading to lower benthic production rates (Cook and Johnson 1974). To estimate the likely API for yoy and one+ sculpins I assumed that the sampling depth coefficients in the regressions for profundal zoobenthic biomass in Rasmussen and Kalff (Table 3, equations 5 to 7) can be used to estimate relative API values in shallow areas (0 to 20 m) and deep areas (20 to 100 m) of deepwater sculpin lakes. The calculations are shown in Table 8. The relative API values obtained were 17.8, 13.8 and 23.8 respectively with a mean 18.4. The mean value was used as a multiplier with the baseline API values estimated using the Randall et al. (1995) equation.

The habitat supply was estimated for a typical deepwater sculpin lake of 1000 ha with a maximum depth of 100 m and a mean depth of 50 m (Table 9). I assumed the one+ population occupied the zone greater than 50 m as reported by Selgeby (1988) in Lake Superior. I assumed the larvae occupied the space in the 8-18 m contours as reported for Lake Michigan by Mansfield et al. (1983). Little is know about spawning in deepwater sculpins apart from the expectation that it will occur over mud. Mansfield et al. (1983) suggested it occurred at >21 m. Selgeby suggested spawning may occur at shallower depths that the normal range during the

winter. Westin (1970) reported *M. quadricornis* spawning at 15-20 m. To complement the assumptions about yoy and one+ habitats, I assumed that spawning took place between 18 and 50 m.

The initial population model was relatively unstable as the estimate yoy survival appeared to be on a knife-edge (Table 10). The population levels changed slowly in scenarios with slightly higher values of yoy survival leading to an increasing population and vice versa. The population size obtained with the total and best estimate baseline habitat supplies were consistent with the limited estimates derived from field observations. In the total habitat supply scenarios changing the API values had no effect indicating that habitat is not the primary constraint on the population. In the best habitat supply scenario increasing the yoy and one+ API values had an effect on population size showing that at those habitat supply levels there is some effect of supply.

All population indicators responded to the same levels of habitat supply reduction (Table 11). In the total baseline the habitat supply levels producing a 95% population were roughly in line with the API values. In the best baseline scenario yoy habitat had the greatest effect followed fairly closely by one+ habitat. As before with lake trout, spawning habitat was only limiting at extremely low levels.

Application of the combined 95% habitat supply levels resulted in nominal drops in predicted population level, 92.9% for total and 97.1% for best scenarios (Table 12). The response of the sculpin model was simpler than seen on the lake trout. Sculpin life history with low fecundity, low adult survival, and limited number of mature age classes means a slow response to any change and a limited capacity to persist.

The results obtained above for lake trout and deepwater sculpin are similar. Using the total habitat supply as a starting point, the percentages of total habitat that must be suitable for spawning, yoy, and one+ life stages to maintain 95% populations are similar:

lake trout – spawning 0.019, yoy 7.047, one+ 95.000
deepwater sculpin - spawning 0.006, yoy, 6.650, one+ 36.720

Hence, preserving small amounts of spawning habitat is of little use unless provision is made for much larger spaces to meet the needs of yoy and one+. While the sculpin case study showed simple parallel responses among population indicators, the lake trout case study shows how interaction among life history processes and habitat supply can produce shifts in which life stage represents the bottleneck for total population success. However, there should be some caution in interpreting these case studies as the results are contingent on uncertainties in the input data, especially in survival from egg hatch to age 1 which is often the least known input.

Discussion

The results obtained with the simple API model in two cases studies showed that it is feasible to develop and implement such models though obtaining estimates of some of the parameters will be a challenge. As with previous work (Minns et al. 1996), the results obtained here strongly indicate a need to re-order priorities for habitat by life stage. Habitat managers often focus on spawning habitat as being essential to population success but these results indicate that yoy and one+ habitat are much more important. No doubt species may exhibit preferences for repeatedly spawning in particular places, a preference that may have a strong inherited or learned component. Those preferences must be considered when designating and protecting habitat supply. Nonetheless habitats suitable for spawning are often much more abundant than needed to ensure sufficient hatched eggs for later life stages. Gunn and Sein

(2000) reporting on experimental removal of spawning habitat in lakes and indicated "lake trout can tolerate substantial losses of spawning habitat". For both lake trout and deepwater sculpin. results suggest that yoy habitat is the most limiting although one+ is a close second. This kind of result can be used to guide the assembly of a essential habitat supply portfolio for a species considering all life stages.

The prototype API model presented here will need further development and application to any particular species will require much more thorough synthesis of available information to secure parameter estimates. Given the various patterns of life history strategy evident in fishes (Winemiller and Rose 1992), examination of several case studies spanning the types should provide further insight into the role of habitat supply. In several areas, it is possible to anticipate future steps: sensitivity analyses, greater structural realism, and application areas. In addition there are basic summarizations and syntheses of existing data and knowledge that can be recommended.

Sensitivity analysis

The sensitivity of the habitat supply requirements to assumptions about population processes and how they may be affected by habitat supply needed to be examined. At least three main areas of examination should be considered:

- The sensitivity of predictions to uncertainty in input parameters can be assessed via Monte Carlo simulations or similar means. I recognize that key life history parameters vary over the distributional range of each species.
- The sensitivity of predictions to model structure needs to be examined. The current prototype implements a simple knife-edge threshold for determining changes in realized survival rates versus the ratio of available to required area per individual. In Moussali and Hilborn (1986), a functional response type equation is used.
- Finally, the sensitivity of predictions to uncertainty due to variability of conditions in ecosystems must be considered. Habitat supply is unlikely to be a constant as fluctuations in climate and hydrology affect the quantity and quality of fish habitats. Higher amounts of habitat will be required to ensure that populations avoid extinction due to habitat supply uncertainty.

Structural realism

The current API model ignores a number of areas already known to be important in fish:

- Fish growth patterns are typically indeterminate and growth rates at different life stages may be density dependent. The growth patterns are fixed in this prototype model but as with survival rates could be linked to suitable habitat supply or other drivers as was done by Minns et al (1996) in a pike population model for Hamilton Harbour.
- The current model only considers three life stages whereas many species have more complex life histories. The basic prototype developed here can be expanded to accommodate more life stages. For example, young-of-the-year often undergo several ontogenetic habitat changes between hatching and reaching age 1.
- The current model ignores male-female differences apart from specifying a proportion of female in the mature population (r). Separate growth and survival schedules can easily be established for male and females where necessary.
- As with growth and sex, an age and size dependent scheme to estimate total fecundity could be implemented where sufficient data are obtainable.

It should be noted however that in many instances such details are lacking for SAR and hence simpler formulations should be the preferred starting point for assessment. The case studies highlight this area. Lake trout is a very well know species and yet precise definitions of the

habitat space for each life stage are not available. The brief survey of the literature on deepwater sculpin illustrated how much less I know of them compared to lake trout.

Potential applications

This API model can be extended to a broader range of questions:

- By replicating the basic model across several discrete spatial units and specifying potential movement rates among units, the dynamics of stocks organized in sub-populations can be examined. This would be applicable to meta-populations, assessment of the potential benefits of reserves and sanctuaries, and the influence of source-sink effects on population size and survival.
- By adding fishing rates, the interactions between habitat supply-driven density dependence and exploitation can be examined. For many fish SAR, this is an important consideration as they are either exploited directly or a by-catch in other directed fisheries. Fishing (F) can be applied in parallel with natural mortality via the year to year transfer of individuals in one+ age classes. For simplicity here, if I assume fishing is applied to the one+ or only mature age classes, the sustained yield will be $F \bullet N_o$ or $F \bullet N_m$. The contribution of fishing to risk of extinction can be assessed and the interaction with spatially-explicit versions examined as well.
- The effect of habitat quality on population success can be examined by the addition of factors affecting life process performance. For example, The mean suitability of non-unsuitable habitat might affect the realization of the maximum potential survival for each life stage. The present model could be modified such that the maximum potential survival is scaled by the mean suitability of all non-unsuitable habitat ($h_i = W_i / (A_T \bullet (1-p_{ui})$). This approach assumes that somewhat suitable habitat can only support a portion of the maximum potential survival rate and is consistent with the ideal free distribution theory. By this addition, the effects of declining or improving habitat quality can be included in population assessments.

Conclusions and recommendations

- Existing population density-body size datasets should be compiled from all sources for all aquatic organisms and analyzed with special attention to stratification by life history characteristics, ecosystem type, taxon, habitat characteristics. These data will allow first order estimates of area habitat requirements of larval, juvenile, and adults for aquatic species-at-risk.
- Existing literature on spawning and egg densities should be compiled from all sources for all aquatic organisms and analyzed for patterns in area-per-individual with respect to life history characteristics, ecosystem type, taxon, habitat characteristics. These data will allow first order estimates of the area habitat requirements of spawning and egg incubation for aquatic species-at-risk.
- Existing data on survival rates in the first year of life (whole or part year) should be compiled from all sources for all aquatic organisms and analyzed with respect to life history characteristics, ecosystem type, taxon, habitat characteristics. The field estimates should be systematically compared with rates estimated from population models and analyses.
- A range of area-per-individual (API) population models should be developed and assessed across the range of life history patterns exhibited in aquatic species-at-risk. The sensitivity of these models to uncertainties of input parameters will help priorize field and experiment efforts to estimate key parameters. The models will also assist in directing efforts to obtain basic life history data for SAR.

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Table 1. Habitat supply and suitability model for each life stage, i = s (spawning), y (young-of-the-year), and o (age one and older).

Variable	Symbol or equation	Expectations
Total area of ecosystem	A_T	
% of total area:		
% Highly suitable	p_{hi}	< 1.0
% Somewhat suitable	p_{si}	< 1.0
% Unsuitable	$p_{ui} = 1 - p_{hi} - p_{si}$	
Habitat suitability (0 to 1)		$h_{hi} > h_{si} > h_{ui}$
High	h_{hi}	1.0
Somewhat	h_{si}	$0.0 < h_{si} < 1.0$
Not	h_{ui}	0.0
Weighted suitable area	$W_i = A_T \bullet (p_{hi} \bullet h_{hi} + p_{si} \bullet h_{si})$	$Wi \approx$ *additive* $\sum Wi <= A_T$
Mean non-zero suitability	$h_i = W_i / (A_T \bullet (1 - p_{ui}))$	$h_i <= 1.0$

Table 2. Life stage population numbers and rate constants for spawning, youing-of-the-year (yoy), and ages one and older (one+), and expectations.

Parameter	Spawning	Young-of-the-year	Ages 1 and older	Expectations
Population number (N)	N_e – eggs deposited N_h – hatched eggs	N_y – yoy end of year 1	N_o – sum of one+ animals N_m – sum of mature animals	$N_e > N_h > (N_y$ and $N_o)$ $N_o > N_m$
Maximum stage survival (s)	s_e - eggs to hatch	s_y – hatch to age 1	s_o – annual rate	$(s_e$ and $s_o) >> s_y$ $s_e > s_o$
Percentage mature females	r			
Fecundity per female$f$)	f			
Age at maturity	m			
Minimum area per individual for maximum survival (a)	a_e – area per egg laid a_s – area per female spawner	a_y – area per yoy (from hatch to age 1)	a_o – area per one+	$(a_o$ and $a_y) >> a_s >> a_e$ $a_o > a_y$

Table 3. Parameter sources and estimation for lake charr, *Salvelinus namaycush*, API model.

Parameter	Estimate(s)	Method	Source
Weight (kg)-length (cm) equation	$5.87 \cdot 10^{-6} \cdot L^{3.18}$	Eq. 3	Shuter et al.1998
Maximum length, L_∞	45 cm	Typical value at ELA Lakes	ditto
Early growth rate, ω	14 cm.year^{-1}	Estimate of size at age 1	ditto
Length at maturity, L_{m50}	38.64 cm	Estimated from eq. 4	ditto
Age at maturity, *m*	6.3 years	Back-calculated using Bertalanffy growth parameters, rounded	ditto
W_∞	1.06 kg	Estimated from previous values	
W_{m50}	0.65 kg	ditto	
W_{geo}	0.83 kg	Geometric mean	
Fry length at emergence	2.5 cm		J.D. Fitzsimons pers. comm.
Percent females, *r*	0.5	Assumed	
Fecundity per kg	1506		Shuter et al. 1998
Fecundity per W_{geo}, *f*	1255		
Egg hatching survival, s_s	0.90		J.D. Fitzsimons pers. comm.
Survival hatch to age 1, s_y	0.0035-0.0055	Upper bound used	Shuter et al. 1998
Annual survival one+, s_o	0.83		Mills et al. 2002
API spawner, a_s	0.5 m^2		J.D. Fitzsimons pers. comm.
API emergent fry	0.13 m^2	Eq. 1	Randall et al 1995
API age 1	10.80 m^2	Eq. 1	Ditto
API yoy, a_y	1.17 m^2	Geometric mean	
API maturity	148.25 m^2	Eq. 1	Ditto
API maximum	219.61 m^2	Eq. 1	Ditto
API one+, a_o	180.44 m^2	Geometric mean	

Table 4. Parameter sources and estimation for lake charr habitat supply model model.

Parameter	Estimate(s)	Method	Source
Lake area	25 ha	Typical ELA lake	Brunskill and Schindler 1971
Maximum depth	20 m	ditto	Mills et al. 2002
Mean depth	10 m	ditto	Brunskill and Schindler 1971
Mean:maximum ratio,a	0.5	calculated	
b	1.0	a/(1-a)	
x	1.78	$(3 \cdot b + \sqrt{(9 \cdot b^2 + 8 \cdot b)})/4$	Minns et al. 1996
Depth range of spawning	0.5-1.5 m	Estimated from graph	Fitzsimons 1994
Depth range for one+	5.0-max m	Estimated hypolimnion in summer	Schindler 1971
Depth range of yoy	1.5-5.0	Assumed to avoid one+ cannibalism	
Area at 0.5 m	24.93 ha		
Area at 1.5 m	24.51 ha		
Area at 5.0 m	20.94 ha		
% in 0.5-1.5 m zone, p_{hs}	0.0169		
% in 1.5-5.0 m zone, p_{hy}	0.1425		
% in 5.0-20.0 m zone, p_{ho}	0.8378		

Table 5. Sensitivity of population numbers predicted in the lake charr API model to change in the API parameters. Non-baseline results are shown as a percentage of the baseline values.

Habitat supply			Scenario	Baseline population numbers			
p_{hs}	p_{hy}	p_{ho}		N_h	N_y	N_o	N_m
1.000	1.000	1.000	Baseline	114076.7	627.4	1774.9	202.0
			50 % a_s	100.0	100.0	100.0	100.0
			200 % a_s	100.0	100.0	100.0	100.0
			50 % a_y	100.0	100.0	100.0	100.0
			200 % a_y	109.3	93.7	97.9	109.3
			50 % a_o	253.6	187.3	195.8	218.6
			200 % a_o	50.1	50.1	50.0	50.0
0.017	0.142	0.838	Baseline	218375.0	166.9	981.7	386.7
			50 % a_s	100.0	100.0	100.0	100.0
			200 % a_s	100.0	100.0	100.0	100.0
			50 % a_y	76.2	198.3	131.7	76.2
			200 % a_y	50.0	50.0	50.0	50.0
			50 % a_o	100.0	100.0	100.0	100.0
			200 % a_o	37.8	100.0	66.0	37.8

Table 6. Reductions in lake trout habitat supply at each life stage required to reduce population indicators to approximately 0.95 of their baseline values.

Habitat varied	p_{hs}	p_{hy}	p_{ho}	Scenario	Population N_h	N_y	N_o	N_m
Total	1	1	1	Baseline	114076.7	627.4	1774.9	202.0
	%	%	%	Target	%	%	%	%
A_s	0.019	100.000	100.000	N_e	95.1	95.1	98.4	107.1
A_s	0.019	100.000	100.000	N_y	95.0	95.0	98.4	107.2
A_s	0.017	100.000	100.000	N_o	85.4	85.4	95.0	123.3
A_s	0.003	100.000	100.000	N_m	13.2	13.2	27.5	95.1
A_y	100.000	7.047	100.000	N_e	95.0	13.2	27.4	95.0
A_y	100.000	50.720	100.000	N_y	107.2	95.0	98.4	107.2
A_y	100.000	45.600	100.000	N_o	123.3	85.4	95.0	123.3
A_y	100.000	7.047	100.000	N_m	95.0	13.2	27.4	95.0
A_o	100.000	100.000	95.000	N_e	95.0	95.0	95.0	95.0
A_o	100.000	100.000	95.000	N_y	95.0	95.0	95.0	95.0
A_o	100.000	100.000	95.000	N_o	95.0	95.0	95.0	95.0
A_o	100.000	100.000	95.000	N_m	95.0	95.0	95.0	95.0
Best	0.017	0.142	0.838	Baseline	218375.0	166.9	981.6	386.7
	%	%	%	Target	%	%	%	%
A_s	2.162	100.000	100.000	N_e	95.0	100.0	100.0	100.0
A_s	0.300	100.000	100.000	N_y	13.2	94.9	94.9	94.9
A_s	0.300	100.000	100.000	N_o	13.2	95.0	95.0	95.0
A_s	0.300	100.000	100.000	N_m	13.2	95.0	95.0	95.0
A_y	100.000	95.000	100.000	N_e	95.0	95.0	95.0	95.0
A_y	100.000	95.000	100.000	N_y	95.0	95.0	95.0	95.0
A_y	100.000	95.000	100.000	N_o	95.0	95.0	95.0	95.0
A_y	100.000	95.000	100.000	N_m	95.0	95.0	95.0	95.0
A_o	100.000	100.000	82.005	N_e	95.0	100.0	97.5	95.0
A_o	100.000	100.000	30.191	N_y	13.2	95.0	45.8	13.2
A_o	100.000	100.000	79.439	N_o	90.0	100.0	95.0	90.0
A_o	100.000	100.000	82.005	N_m	95.0	100.0	97.5	95.0

Table 7. Summary of lake trout population predictions in relation to habitat supply constraints.

Baseline	Habitat supply			Population			
	Spawning	YOY	One+	Hatched eggs	Age 1 recruits	One+	Mature
Total	1	1	1	114076.7	627.4	1774.9	202.0
Best	0.017	0.142	0.838	218375.0	166.9	981.6	386.7
95% Total	0.000192	0.07047	0.95	108372.5	82.8	487.2	191.9
95% Best	0.000051	0.1349	0.687	28802.3	158.4	931.8	367.1
% Total	0.019	7.047	95.000	95.0	13.2	27.4	95.0
% Best	0.300	95.000	81.981	13.2	94.9	94.9	94.9

Table 8. Parameter sources and estimation for deepwater sculpin, *Myoxocephalus thompsoni*, API model.

Parameter	Estimate(s)	Method	Source
Weight (g)-length (mm) equation	$10^{-6.009} \cdot L^{3.5512}$		Selgeby 1988
Maximum length, L_∞	14 cm	Lake Superior	ditto
Early growth rate, ω	4.1 cm.year^{-1}	Estimate of size at age 1	ditto
Length at maturity, L_{m50}	7.4 cm	Estimated from eq. 4	ditto
Age at maturity, m	3 years	Observation	ditto
W_∞	40.96	Calculated	
W_{m50}	4.26	Calculated	
W_{geo}	13.20	Calculated	
Fry length at emergence	0.6 cm	5.5-6.5 mm	Selgerby 1988
Percent females, r	0.5	Quoted from Jacobs (1953)	Parker 1988
Fecundity per kg	-		
Fecundity per W_{geo}, f	481	Quoted from Jacobs (1953)	Parker 1988
Egg hatching survival, s_s	0.90	Used lake charr #	
Survival hatch to age 1, s_y	0.03	Derivation in text	
Annual survival one+, s_o	0.323	Z = 1.13	Selgeby 1988
Benthic multiplier	18.437	Derivation in text	
API spawner, a_s	0.283 m^2	Male M. quadricornis defends 0.3 m radius	Westin 1969.
API emergent fry	0.003 m^2	Eq. 1	Randall et al 1995
API age 1	0.454 m^2	Eq. 1	Ditto
API yoy, a_y	0.702 m^2	Geometric mean* multiplier	
API maturity	2.08 m^2	Eq. 1	Ditto
API maximum	10.80 m^2	Eq. 1	Ditto
API one+, a_o	87.47 m^2	Geometric mean*multiplier	

Table 9. Parameter sources and estimation for deepwater sculpin habitat supply model model.

Parameter	Estimate(s)	Method	Source
Lake area	100 ha	Typical lake	
Maximum depth	100 m	ditto	
Mean depth	50 m	ditto	
Mean:maximum ratio,a	0.5	calculated	
b	1.0	a/(1-a)	
x	1.78	$(3 \cdot b + \sqrt{(9 \cdot b^2 + 8 \cdot b)})/4$	Minns et al. 1996
Depth range of spawning	18-50	15-20 m M. quadricornis Assumed to be between yoy and one+ ranges	Westin 1970
Depth range for one+	50-max m	Lake Superior	Selgeby 1988
Depth range of yoy	8-18 m	Inshore over 8-18 m Lake Michigan	Mansfield et al 1983
Area at 8 m	97.78 ha		
Area at 18 m	90.78 ha		
Area at 50 m	50.26 ha		
% in 18-50 m zone, p_{hs}	0.4052		
% in 8-18 m zone, p_{hy}	0.0700		
% in 50-100 m zone, p_{ho}	0.5026		

Table 10. Sensitivity of population numbers predicted in the deepwater sculpin API model to change in the API parameters. Non-baseline results are shown as a percentage of the baseline values.

Habitat supply			Scenario	Baseline population numbers			
p_{hs}	p_{hy}	p_{ho}		N_h	N_y	N_o	N_m
1.000	1.000	1.000	Baseline	1020050.3	30601.5	45179.8	4712.6
			50 % a_s	100.0	100.0	100.0	100.0
			200 % a_s	100.0	100.0	100.0	100.0
			50 % a_y	100.0	100.0	100.0	100.0
			200 % a_y	100.0	100.0	100.0	100.0
			50 % a_o	100.0	100.0	100.0	100.0
			200 % a_o	100.0	100.0	100.0	100.0
0.405	0.070	0.503	Baseline	997829.1	29914.5	44186.9	4610.0
			50 % a_s	100.0	100.0	100.0	100.0
			200 % a_s	100.0	100.0	100.0	100.0
			50 % a_y	102.2	102.3	102.2	102.2
			200 % a_y	50.0	50.0	50.0	50.0
			50 % a_o	100.0	100.0	100.0	100.0
			200 % a_o	61.2	61.3	61.2	61.2

Table 11. Reductions in deepwater sculpin habitat supply at each life stage required to reduce population indicators to approximately 0.95 of their baseline values.

Habitat varied	p_{hs}	p_{hy}	p_{ho}	Scenario	Population N_h	N_y	N_o	N_m
Total	1	1	1	Baseline	1020249.7	30607.5	45188.6	4713.6
	%	%	%	Target	%	%	%	%
A_s	0.006	100.000	100.000	N_e	95.0	95.0	95.0	95.1
A_s	0.006	100.000	100.000	N_y	95.0	95.0	95.0	95.1
A_s	0.006	100.000	100.000	N_o	95.0	95.0	95.0	95.0
A_s	0.006	100.000	100.000	N_m	94.9	94.9	95.0	95.0
A_y	100.000	6.799	100.000	N_e	95.0	94.9	95.0	95.0
A_y	100.000	6.805	100.000	N_y	95.1	95.0	95.1	95.1
A_y	100.000	6.801	100.000	N_o	95.0	95.0	95.0	95.0
A_y	100.000	6.799	100.000	N_m	95.0	94.9	95.0	95.0
A_o	100.000	100.000	37.553	N_e	95.0	95.0	95.0	95.0
A_o	100.000	100.000	37.553	N_y	95.0	95.0	95.0	95.0
A_o	100.000	100.000	37.540	N_o	95.0	95.0	95.0	95.0
A_o	100.000	100.000	37.553	N_m	95.0	95.0	95.0	95.0
Best	0.405	0.07	0.503	Baseline	997829.1	29914.5	44186.9	4610.0
	%	%	%	Target	%	%	%	%
A_s	0.015	100.000	100.000	N_e	94.8	94.9	94.9	94.9
A_s	0.015	100.000	100.000	N_y	94.9	95.0	95.0	95.0
A_s	0.015	100.000	100.000	N_o	94.9	95.0	95.0	95.0
A_s	0.015	100.000	100.000	N_m	94.9	95.0	95.0	95.0
A_y	100.000	95.000	100.000	N_e	95.0	95.0	95.0	95.0
A_y	100.000	95.000	100.000	N_y	95.0	95.0	95.0	95.0
A_y	100.000	95.000	100.000	N_o	95.0	95.0	95.0	95.0
A_y	100.000	95.000	100.000	N_m	95.0	95.0	95.0	95.0
A_o	100.000	100.000	73.022	N_e	95.0	95.1	95.1	95.0
A_o	100.000	100.000	72.962	N_y	94.9	95.0	95.0	94.9
A_o	100.000	100.000	72.982	N_o	95.0	95.0	95.0	95.0
A_o	100.000	100.000	73.022	N_m	95.0	95.1	95.1	95.0

Table 12. Summary of deepwater sculpin predictions in relation to habitat supply constraints.

Baseline	Habitat supply			Population			
	Spawning	YOY	One+	Hatched eggs	Age 1 recruits	One+	Mature
Total	1	1	1	1020249.7	30607.5	45188.6	4713.6
Best	0.405	0.07	0.503	997829.1	29914.5	44186.9	4610.0
95% Total	0.0000619	0.0665	0.3672	946873.1	28406.2	41958.9	4377.5
95% Best	6.336E-05	0.068	0.3755	969206.5	29059.8	42924.4	4478.3
% Total	0.006	6.650	36.720	92.8	92.8	92.9	92.9
% Best	0.016	97.143	74.652	97.1	97.1	97.1	97.1

Figure 1. Stage survival rate (si) as a function of area per individual entering the life stage (A_i).